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Population-level responses of the mummichog, Fundulus heteroclitus, to chronic nutrient enrichment in a New England salt marsh

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POPULATION-LEVEL RESPONSES OF THE MUMMICHOG, *FUNDULUS HETEROCLITUS*, TO CHRONIC NUTRIENT ENRICHMENT IN A NEW ENGLAND SALT MARSH

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TABLE OF CONTENTS

ABSTRACT

Mummichog (*Fundulus heteroclitus*) responses to chronic whole-ecosystem nutrient enrichment were examined near Plum Island Sound, Massachusetts. Dissolved fertilizer was released into replicate salt marsh creeks over 6 growing seasons to simulate agricultural run-off (bottom-up effects). Density, biomass, secondary production, growth rate, and condition factor were estimated in fertilized and reference creeks. Mummichog densities were also used to determine if mummichog growth or health varied with density. Over 7,600 mummichogs were marked and released into the treatment and control areas to measure responses. Over 900 mummichogs were recovered. Mummichog abundance was higher ($p = 0.055$) in nutrient-enriched creeks than reference creeks (0.81 ± 0.04 fish m^{-2} and 0.59 ± 0.07 fish m^{-2} respectively). Nutrient enriched-creek biomass of 522.9 ± 36.1 mg dw m^{-2} was significantly higher ($p=0.028$) than control-creek biomass of 338.5 ± 26.7 mg dw m^{-2}. However, reference-creek growth rates of 0.105 ± 0.091 were significantly higher ($p=0.04$) than the nutrient enriched-creek growth rates of 0.073 ± 0.065 mm d^{-1}. Secondary production and condition factor of mummichogs did not differ with nutrient enrichment. Nutrient enrichment likely stimulated primary production causing bottom-up effects in the food web, which increased mummichog abundance and biomass. However, as abundance increased, mummichog growth rates decreased, suggesting a density-dependent response,

likely caused by either intraspecific competition or behavioral changes causing dietary shifts.

1 - INTRODUCTION

Top-down and bottom-up forces and their effect on food webs have been the source of a longstanding ecological debate (Hairston et al. 1960; Valiela et al. 2004). Ecologists often study top-down and bottom-up effects with the goal of understanding the fundamental controls over ecosystem structure and function.

Bottom-up effects occur when nutrients limit primary production and restrict ecosystem energy flow at the base of the food web (Valiela et al. 2004; Cain et al. 2008). A simple example would be a marine environment so depleted of nutrients that the growth of primary producers like phytoplankton and benthic algae becomes limited. This would then limit the growth of secondary consumers like fish and invertebrates.

Top-down effects occur when predators limit lower trophic levels in an ecosystem by controlling the population size, biomass, or growth of these organisms (Valiela et al. 2004; Cain et al. 2008). A simple example from a marine environment would be fish controlling and limiting the abundance and growth of benthic algae or zooplankton by direct effects of predation or indirect effects by preying on intermediate organisms.

Understanding these two contrasting effects is becoming increasingly important as an aid in preserving ecosystems exposed to anthropogenic effects. Human activity and involvement in previously

unmodified environments can significantly change these ecosystems by altering the nature of the controlling forces.

Estuaries and associated salt marshes are commercially and ecologically important because of their high levels of primary and secondary production. Estuaries provide over 50% of the commercial fisheries in the United States (Houde and Rutherford 1993; Deegan 2002). Estuaries are also important nurseries for fish species, with over 25% of US east coast fish species spending some part of their life history in estuaries (Houde and Rutherford 1993; Deegan 2002). These important ecosystems and other coastal areas are being influenced by human agricultural activity, most commonly by nutrient enrichment from run-off, as well as other anthropogenic processes such as sewage treatment and industrial activities (Valiela et al. 2004). Eutrophication occurs when nutrient enrichment of a body of water stimulates algal growth (NOAA 1999). This can be a natural process, for example when nutrient-rich water enters coastal areas from tidal movements. However, as human population growth has increased in coastal areas in recent decades, cultural eutrophication has occurred from human activities. A report detailing North American estuaries found 67% of the estuarine area observed is moderately to highly eutrophic, experiencing oxygen deprivation, vegetation loss, or other hypoxic conditions (NOAA 1999). This report also predicts that coastal eutrophication will worsen in the next 10 years because of the

growing human population in coastal areas. Adding nutrients, specifically nitrogen, to these systems increases primary production and can decrease or alter secondary production of nekton and benthos (NOAA 1999; Deegan 2002; Deegan et al. 2007). Environmental problems that cause altered secondary production include animal dietary shifts, submerged vegetation loss, plant community changes, habitat loss, and oxygen depletion from the increased primary production and excess organic carbon decomposition (NOAA 1999; Deegan 2002; Valiela et al. 2004; Powers et al. 2005). The resulting increased algal growth and altered nekton abundance can change food-web interactions and ultimately impair commercial and recreational fishing. This occurs when some species are more susceptible than others to the negative effects of eutrophication or when species benefit too much from the added production.

Because of the high level of production in estuaries, they face constant human environmental pressure. As the proportion of humans living near the coast continues to grow, nekton consumers face an increasing threat of overfishing, both commercial and recreational. Overfishing is most likely the cause of many estuarine fishery declines, by altering natural abundances of local fish and invertebrate species (Houde and Rutherford 1993). The decrease in abundance from overfishing also alters top-down interactions of local coastal food webs (Jackson et al. 2001). Overfishing may affect

estuaries more so than any other marine ecosystem due to the high amount of fisheries that come from estuaries (Jackson et al. 2001).

Eutrophication does not always lead to decreases in secondary production. Increases in abundance from elevated primary production can accompany eutrophication in the absence of hypoxia (Nixon and Buckley 2002). Nekton abundance increases can lead to increased commercial and recreational overfishing as well as fishing selectivity for specific size classes or species (Breitburg et al. 2009). Fishing pressure may remain at high levels even as production begins to slow from decreasing nutrient levels or hypoxia. Overfishing and eutrophication can combine to amplify the negative effects in estuaries associated with each of these threats (Jackson et al. 2001; Breitburg et al. 2009). Potential synergistic effect between overfishing and eutrophication can negatively impact marine environments by increasing primary production, degrading or eliminating habitat, and decreasing consumers. One such example of the synergistic effects of nutrient enrichment and overfishing are depleted oyster reefs. Some oyster reefs on the east coast of the United States are unable to exert top-down control over primary producers (i.e., phytoplankton) due to their decreasing biomass from over-harvesting (Jackson et al. 2001). This facilitates overproduction of the primary producers, specifically algae. Little is known of the potential synergistic effects associated with nekton

in estuaries because few studies have been able to examine both nutrient enrichment and overfishing together on the same time scale.

Eutrophication and overfishing of salt marshes and estuaries both need to be critically studied to gain a better understanding of estuarine biotic responses. While nutrient enrichment may increase nekton abundances in the short term (Nixon and Buckley 2002), not enough is known about long-term ecological impacts. Long-term, chronological studies, simulating the way most stressors occur in nature, are among the best ways to study these environmental issues. The long-term effects are of most concern because many eutrophication and overfishing episodes in nature take time to develop. Eutrophication and overfishing are two good examples of bottom-up and top-down effects, respectively. A long-term study of these issues was addressed in the NSF-funded TIDE program (Trophic cascades and Interacting control processes in a Detritus-based aquatic Ecosystem).

TIDE is currently being conducted in the northeast United States near the Plum Island Sound, Massachusetts (Deegan et al. 2007; Fleeger et al. 2008). TIDE began in 2003 and will continue at least through the summer of 2011. The project entails whole-ecosystem nutrient enrichment throughout each growing season (May-September) from 2004 to the present in two formerly non-enriched creeks (< 4.5 µm NO_3^- and < 1.2 µm PO_4^{3-} / L, Deegan et al. 2007). Two additional creeks serve as references without nutrient enrichment with the same background

nutrient levels as mentioned above. Comparisons between the fertilized and unfertilized creeks entail a test for bottom-up effects to better understand coastal eutrophication in salt marshes. In combination with the nutrient addition, whole-creek fish reduction treatments are also conducted. These reductions are paired with areas of unmanipulated fish abundances, to examine top-down control by a high-level saltmarsh predator, the mummichog (*Fundulus heteroclitus*). Fish reductions are adequate to simulate altered abundances occurring in nature as a result of overfishing of high-level predators. The experimental treatments are applied in a factorial design allowing for the potential interactions between nutrient enrichment and predator control to be examined. These two treatments provide an opportunity to study Atlantic coast saltmarsh systems to compare the relative strength of and potential interactions between bottom-up controls (of benthic invertebrates and microalgae) through nutrient enrichment and top-down controls. Because the manipulations extend across marsh habitats types, effects at the landscape level may be observed.

Atlantic coast saltmarsh primary producers include two *Spartina* species, phytoplankton, and benthic algae (Deegan 2002). Benthic invertebrates link the primary producers and detritus to nekton consumers. The nekton consumer of most importance in the TIDE study is the mummichog, (*Fundulus* heteroclitus), comprising ~1/5 of the nekton abundance and almost all of the fish abundance (Deegan et al. 2007).

The mummichog is a small killifish ranging in total length from 15 (as post larva) to > 120 mm (Deegan et al. 2007; Kneib 2009). Mummichogs are a crucial predator and an important prey species in Atlantic coast saltmarsh systems from Newfoundland to northern Florida (Kneib and Stiven 1982; Allen et al. 1994). Mummichogs are the dominant fish species in Plum Island Estuary (PIE) salt marshes, where TIDE is conducted, making up 19% of the nekton abundance and 92% of the fish abundance (Deegan et al. 2007; Hagan et al. 2007). Mummichogs also make up 41% of the nekton biomass and 89% of the fish biomass in PIE (Deegan et al. 2007). When compared to fish species in other environments, mummichog biomass is extremely high (Kneib 1986; Deegan et al. 2007). The high mummichog biomass could indicate strong top-down predation effects in Atlantic coast saltmarsh systems.

The mummichog life cycle, including feeding, refuge, and reproduction occur solely in salt marshes (Allen et al. 1994; Hagan et al. 2007). Mummichogs feed in creeks, ditches, and on the intertidal marsh surface during high tide (Allen et al. 1994; Teo and Able 2003). Mummichogs have been observed entering creeks, ditches, and intertidal zones with empty stomachs on flooding tides and leaving with full stomachs on ebbing tides (Kneib 1986; Allen et al. 1994). Mummichogs are opportunistic omnivores that feed on plant material, benthic microalgae, detritus, and benthic invertebrates like small crustaceans, annelids, and terrestrial insects (Kneib and Stiven 1978;

Allen et al. 1994; Deegan et al. 2007). Larger adult mummichogs (≥ 40 mm TL) prey on grass shrimp (*Palaemonetes pugio*), various amphipods, snails, and other smaller mummichogs. The gut contents of small (< 40 mm TL) and large mummichogs differ because of differences in predator and prey body size and prey availability (Kneib 1986; Kneib 1988; Allen et al. 1994).

Mummichogs spawn on the intertidal platform in association with the large spring tidal cycles (Taylor 1999; Burnett et al. 2007). Mummichogs lay eggs at or near the spring high-tide water mark. Eggs are laid in algal mats, on plant stems, or buried in the sand. Eggs are incubated aerially above water and fully develop during the 9-15 days between the spring tidal cycles. The following spring tide (~2 weeks later) submerges the eggs, which triggers hatching. Clutch size is normally less than 50 eggs in *Spartina alterniflora*-dominated marshes (Taylor 1999). Juveniles ($\leq$ 40 mm TL) often remain in small pools, depressions, or ponds on the intertidal marsh platform. Once a larger size is achieved, mummichogs make their way into larger ponds, ditches, the marsh edge, and intertidal creeks (Able et al. 2006).

For my master's thesis I conducted a large-scale mark and recapture study of mummichogs in PIE. The mark and recapture study was conducted in association with the TIDE project during the summer of 2009, the 6th year of nutrient enrichment when chronic nutrient enrichment effects may be occurring. The environmental manipulations

associated with TIDE may have altered mummichog abundance, biomass, production, growth, and/or health (Weis et al. 2001; Teo and Able 2003). The study also helps to better understand the food web and possible synergistic response to the TIDE treatments. Flume net collections of mummichogs on the marsh platform at high tide were used to augment the mark and recapture study.

Estimates of abundance, biomass, production, individual growth rates, and fish condition were all made to quantify the possible effects of nutrient enrichment. Abundance (expressed as fish per treatment area, or creek reach) was measured from the mark and recapture study, and density (expressed as fish per m^2) was measured from the flume net collections. Biomass, secondary production, and growth rates were estimated using the mark and recapture study. A separate sample of mummichogs was collected to examine fish health via Fulton's condition factor (Nash et al. 2006) among TIDE treatments.

The first and overarching question addressed was (1) Does nutrient enrichment effect the mummichog population in PIE? The answer to this question may follow a similar pattern among the various dependent variables (abundance, biomass, production, growth rate, and health) measured. My null hypothesis is the nutrient enrichment treatment will not affect mummichog abundance, biomass, production, growth rate, or health. If the null hypothesis is rejected, an alternate hypothesis would be that nutrient enrichment increases

primary production as a bottom-up effect. Increasing primary production would increase the amount of food available to the mummichog population. This would likely lead to increases in abundance, biomass, production, and growth rate. Abundance and biomass would increase because more food is available to support a larger population of mummichogs. Production and growth rates would be higher because more food is available for fish to consume and use as an energy source. Condition would also likely increase as fish would be heavier and healthier because of the increase in food.

Other questions being addressed include: (2) Does abundance effect mummichog growth rate and/or health? and (3) Does landscape type effect mummichog growth rate and/or health? My null hypothesis for question (2) is mummichog growth rate and/or health will not be affected by mummichog abundance. If I am able to reject my null hypothesis regarding growth rate and mummichog abundance, I would expect faster growth rates in areas with fewer mummichogs. A common cause of such an effect would be a reduction in intraspecific competition for food and space when fewer fish are present. If I reject my null hypothesis regarding health and mummichog abundance, I would expect healthier mummichogs in areas with fewer fish. This would be due to reduced intraspecific competition for food and space when fewer fish are present and more food is available to fewer mummichogs.

My null hypothesis for question (3) is mummichog growth rate and/or health will not be affected by landscape type. In a recent study landscape effects were measured by the complexity of the drainage systems attached to creek systems (Kneib 2009). Mummichogs in simple drainage networks had higher growth rates than mummichogs living in complex drainage networks. Complexity was measured as the linear amount of tidal channel edge within a treatment area. Marshes closer to large channels commonly have a simpler drainage network. I studied two landscape conditions associated with the first-order tidal creeks used in my study. Creeks were divided into two sections (or reaches), an upper reach and a lower reach. The upper reach was closest to the upland forest and consists of narrower creek channels experiencing low water conditions for longer time periods during low tide. The lower reach has higher water flow and wider creek channels with longer duration of tidal flooding.

2 - METHODS

2.1 - Study Site

My thesis research was conducted in association with the TIDE project during the summer of 2009. The study site is located near the Plum Island Sound in northeastern Massachusetts, 42.73' N, 70.84' W (Figure 1). The study site was specifically located in 4 first-order saltmarsh creeks which ultimately flow into the Rowley River (Table 1). The creeks were chosen for similarities in physical characteristics (e.g., substrate, tidal amplitude, and physiognomy), size, and vegetation. Creek walls and beds are exposed to air at low tide in PIE with the exception of small, haphazardly located intertidal pools. *Spartina alterniflora* is found in a 3-4 m wide band along the creek-marsh edge. Mosquito ditches built in the 1940's are found in all creek systems in this study. The high marsh is characterized by expansive areas of *Spartina patens* as well as permanently flooded salt-marsh pannes, which are replenished with new tidal water on spring high tides at ~2 week intervals. Tidal amplitudes in PIE can reach ~4 m during spring high tides and ~2.5-3 m during neap high tides.

2.2 - Sampling Procedure

2.2.1 – TIDE Treatments

The TIDE project entails two whole-ecosystem (at the landscape level) treatments. The first treatment is a nutrient-enrichment

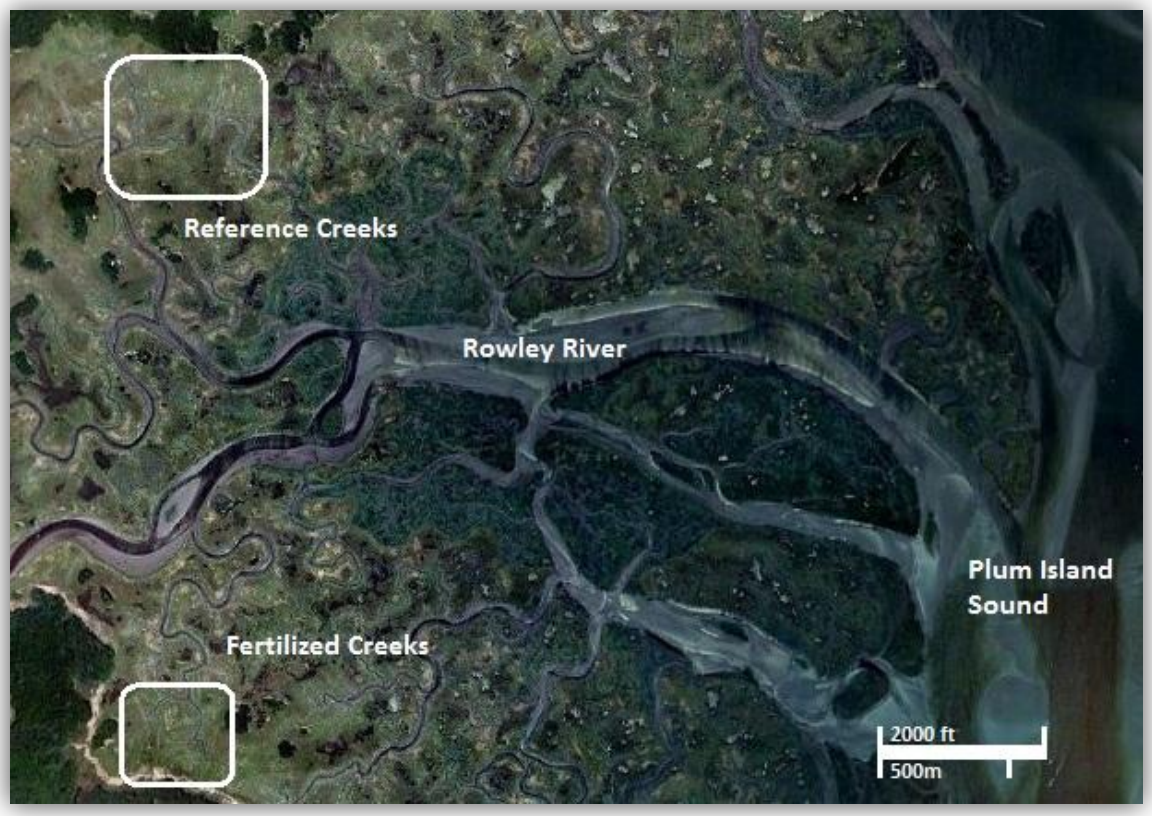

Figure 1. An aerial photo of the study site. This marsh is located in the Rowley River drainage which drains into the Plum Island Sound in northeastern Massachusetts.

Table 1. The physical characteristics of the each creek used in the study. Each creek was divided by a fish block into two similar creek reaches.

Creek	Total Watershed Area (m^2 x 10^4)	Linear Distance (m)	Distance from Rowley River (km)	Distance from Plum Island Sound (km)	Volume (L x 10^6)	Cross-sectional area (m^2)
Reference 1	6.01	260	1.28	3.74	1.37	5.27
Reference 2	5.32	230	1.43	3.89	2.04	8.89
Fertilized 1	5.91	300	1.31	4.43	3.73	12.42
Fertilized 2	6.59	335	1.31	4.43	3.59	10.73

treatment applied to 2 creeks. Nutrient enrichment in these 2 creeks has occurred annually since 2004. The growing-season long treatment is intended to improve our understanding of the long-term, cumulative effects of eutrophication. The fertilization treatment is applied from ~June 1st – September 15th each year. These creeks are nutrient enriched with target concentrations in water with the flooding tide of 50-70 µmol NO_3^- / L and 4 µmol PO_4^{3-} / L. The nutrients are obtained from commercially available fertilizer, N from $NaNO_3$ and the P from NaH_2PO_4. These concentrations are consistent with those in estuaries experiencing moderate to high eutrophication (Deegan et al. 2007). The fertilization is achieved by first mixing fertilizer with ambient creek water in a large holding tank. The nutrient-enriched water is pumped into two creeks on each rising tide (i.e., twice daily) which then inundates the creeks and surrounding marsh landscape. A computer program controls the pumps that deliver nutrient-rich water at the correct levels necessary to achieve a constant concentration in flooding water. The two remaining creeks serve as reference creeks. These creeks experience background levels of nutrients at ~3.5 µmol NO_3^- and ~0.9 µmol PO_4^{3-} / L (Deegan et al. 2007).

The second treatment associated with the TIDE project is a fish (i.e., mummichog) manipulation treatment intended to mimic the effects of overfishing on a high-level predator. In each of the 4 creeks, a block-net made of 6.35-mm mesh Vexar is constructed across the width

of the creek to restrict access of fish to the upper reach on a rising tide. The block-net divides each creek into two separate areas, a reference fish area and a manipulated fish area. Minnow traps are fished behind the block-net to reduce mummichog abundance. The experimental design was a split plot design with 2 nutrient-enriched creeks (with nutrient enrichment as the main effect) and 2 reference creeks each subdivided into a reference fish area and a manipulated fish area as the subplot. A mummichog reduction of 60% was achieved in 2004 and 2005 during TIDE research (Deegan et al. 2007), although larger fish ($\geq$ 40 mm TL) were more efficiently reduced than smaller (< 40 mm TL) fish. Smaller fish are able to penetrate the block net and avoid capture due to the mesh size of the block net and the size of the holes in the minnow trap. During spring high tides when the platform is flooded, fish are able to navigate around the block net; therefore, minnow traps must be constantly fished to obtain a reduction. Although fish blocks were implemented, fish abundance reduction proved ineffective in 2009 during the course of my experiment (Deegan, personal communication), probably because the use of minnow traps was minimized during the mark and recapture effort. Instead, a lower reach (creek area below the block-net) and an upper reach (creek area above the block-net) were considered as part of the experimental design. Thus, 8 creek reaches were studied in a similar experimental design (Figure 2). For more information on the TIDE

project and the application and results of these treatments see Deegan et al. (2007).

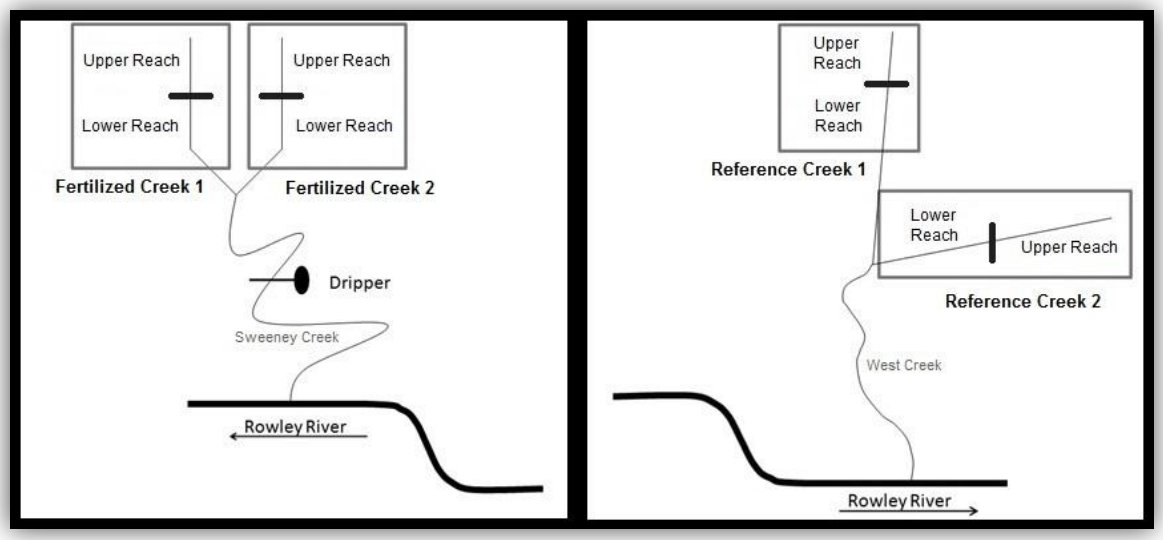

Figure 2. TIDE experimental design. Each of the 4 creeks is divided into an upper creek reach and a lower creek reach. The dripper is the point of the nutrient release.

2.2.2 – Mark and Recapture Study

A mark and recapture study of mummichog was conducted from July 7th until September 15th, 2009, in the 6th year of nutrient additions. From mark and recapture data, abundances (defined as the number of fish in a watershed), biomass, secondary production, and growth rates of *Fundulus heteroclitus* were estimated. Mummichog abundance was converted to density (fish m^{-2}) on a per creek basis.

Fish were captured and marked July 7th through July 17th. Fish were collected each day for marking during an ebbing tide using minnow traps. At each creek reach, 12-20 minnow traps were placed evenly across the span of the reach. Over 99% of the fish collected and

marked were ≥ 40 mm TL. Fish ≥ 40 mm TL are considered adults with different diets than the smaller juveniles, justifying the choice in size classes. The design of the minnow traps (which allowed mummichogs < 40 mm TL to escape) and high stress-related tagging mortality in smaller fish (Able et al. 2006) also precluded use of smaller mummichogs in the mark-recapture procedure. The number of fish collected varied from ~300 to ~1100 each day. Fish were gathered from multiple creek reaches each day and brought back to the Marine Biological Laboratory (MBL) Marshview Field Station. Fish were held in plastic tubs with aerators during transport (~15-45 minutes) and during the tagging procedure (~3-6 hours). Each fish was anesthetized, measured (to the nearest millimeter of total length (TL)), paint tagged, and coded-wire tagged. Paint tags were used as a visual cue to facilitate recapture. Fish were paint tagged and coded-wire tagged in opposite sides of the body in the dorsal musculature. Decimal Coded Wire Tags manufactured by Northwest Marine Technology were used to identify fish and ultimately to obtain growth rates of individuals. Due to the design of the wire tags, an archive was kept to later obtain the date of release and beginning length. This was done by injecting every 3rd tag into a strip of silicone caulk. Fish were held an additional 2 h to ensure survival and allow for recovery from the stress of the tagging procedure. Mortalities were enumerated and dead fish were removed from the holding tank.

Marked fish were released after the 2-h recovery period into the same creek reach where they were captured. The home range of small mummichogs has been found to be typically less than 30 m (Able et al. 2006), so the release area should be familiar to reduce stress. Fish were released at high tide to avoid stress that may occur in small pools at low tide.

The recapture effort began on July 27th, 2009, 10 days after the last capture and marking day and ended September 15, 2009 when the nutrient-enrichment treatment ended. Fish were recaptured using minnow traps in a similar manner to how fish were collected for tagging. All fish collected were passed through a Northwest Marine Technology V-Detector which detects the presence of the Decimal Coded Wire Tags. Each marked mummichog was then placed on ice in the field and frozen in a -20° freezer upon return to the field station. Fish were later shipped to Louisiana State University for processing.

2.2.3 – Flume Net Estimates

Flume nets were used to obtain an independent density estimate of nekton using the salt-marsh platform during nighttime spring high tides which occur twice daily for 1-3 days every ~2 weeks. Flume nets were built on the marsh platform near the creek edge. Two replicate flume nets were constructed in each of the 8 creek reaches (i.e., upper and lower reach in each creek). During spring high tides, the marsh platform is flooded up to ~1 m allowing marsh nekton to forage

on the platform. The flume nets used in this study (Deegan et al. 2007) were different from traditional flume nets in that a known area is sampled (McIvor and Odum 1986). Flume nets were 2 m wide located at the edge of the *Spartina alterniflora* zone and extended 5 m in length into the *Spartina patens* zone. They were constructed with of 4.76-mm mesh netting. The long side of the net was raised before the tide reached the nets. The shorter "back" and "front" nets were attached at slack high tide completely sealing the entire 10 m^2 flume net. Nekton followed the receding tide to the front of the net where they were collected upon return to the field. Mummichogs were sorted out from the resulting nekton sample, then enumerated, measured, and weighed (wet weight). Mummichog flume net density and biomass were estimated as fish per m^2 and grams per m^2 respectively, and averaged for each creek reach. Flume nets retain all post-larval mummichogs ≥ 15 mm TL. Two size class densities were then estimated for all post larval and ≥ 40 mm TL mummichogs. Samples were taken in the months of June, July, and August. The August flume net sample dates corresponded most closely to the mark and recapture study dates; therefore, the August flume net data was used in comparisons.

2.3 - Data Analysis

2.3.1 - Mark-Recapture Abundance and Density

Mummichog abundance was estimated using data from the first 2 weeks of the recapture effort during the mark and recapture study.

During this time, both marked and unmarked fish were enumerated upon capture in minnow traps. The mark-recapture method used to estimate abundance was based on the "Peterson estimate" or "Lincoln index" (Seber 1972). Assumptions were a closed population (no migration), an equal probability of capture of marked and unmarked fish, equal mortality and recruitment of marked and unmarked fish, and that all marks/tags are retained. Roughly 12-20 minnow traps were placed evenly across each creek reach during the two-week recapture period in a similar pattern as the initial capture. Abundances from each minnow-trap collection were estimated and averaged to generate a creek reach mean and 95% confidence intervals. I attempted to estimate abundance at all 8 creek reaches; however, due to a low resampling efficiency in one of the creek reaches, only 7 creek reaches were estimated (the upper reach in fertilized creek 2 did not have an abundance measurement, see Figure 2). Abundance of mummichogs ≥ 40 mm TL for each creek reach was calculated using equation (1).

$$\text{Eq. (1)} \quad A_{\geq 40} = (T_{Marked} * R_{unmarked}) / R_{Marked}$$

In Eq. (1) $A_{\geq 40}$ is the abundance of mummichogs ≥ 40 mm TL, T_{Marked} is the total number of marked mummichogs released in the creek reach, $R_{unmarked}$ is the total number of mummichogs caught without a tag, and R_{Marked} is the total number of marked mummichogs recaptured.

Abundance measurements from the mark-recapture study from each creek were converted into a density (mummichogs m^{-2}) measurement using

the watershed areas for each creek (see Table 1). Density measurements were calculated on a per creek basis (n = 4) because exact watershed areas of each individual creek reach were not known. Watershed areas for each whole creek were derived by using a known watershed area from Deegan et al., 2007 and adjusting it for the linear distance of the working section of each first-order creek.

$$\text{Eq. (2)} \quad D_{\geq 40} = A_{\geq 40} / W_A$$

In Eq. (2) $D_{\geq 40}$ is the density of mummichogs ≥ 40 mm TL in each creek, $A_{\geq 40}$ is the abundance of mummichogs ≥ 40 mm TL, and W_A is the Watershed Area of the working section of each creek as m^2.

Densities in each creek were estimated as mummichogs m^{-2} as described in Eq. (2). A single density estimate was made for each creek, and error terms and degrees of freedom were based on creel level replication (2 nutrient-enriched and 2 reference creeks). A t-test performed in SAS version 9.2 was used to compare mean fish densities among nutrient-treated (n = 2) and reference creeks (n = 2).

2.3.2 – Flume Net Density

Flume net density was measured as mummichogs m^{-2}. Two measurements were taken at each creek reach for two size classes of the population that included all post-larval mummichogs (≥ 15 mm TL) and mummichogs ≥ 40 mm TL.

To test for nutrient-enrichment treatment effects, flume net densities (mummichogs m^{-2}) of all post-larval mummichogs and mummichogs

≥ 40 mm TL on the marsh platform were analyzed separately using a split plot mixed model analysis of variance (ANOVA) in SAS 9.2. Nutrient treatment and creek reach were considered fixed effects and the creek replication was considered a random effect.

2.3.3 - Measurement Correlation

The two independent density estimates (from the mark and recapture study and from flume nets) for mummichogs ≥ 40 mm TL were compared with a Spearman's rank correlation coefficient test using Sigma Plot version 9.0. The 7 of 8 creek reach abundances from the mark and recapture study were compared to the flume net densities in the same corresponding reaches.

2.3.4 - Length Distributions

Initial fish lengths from the mark and recapture study were used to compare body-size distributions in the nutrient-enriched and reference creeks. Initial lengths were obtained from the archive kept during the mark and recapture study; 7,828 individual lengths were thus obtained. Because both fertilized and reference-creek distributions were skewed to the right, they were analyzed in SAS 9.2 using a two-sample Kolmogorov-Smirnov test as opposed to a t-test.

2.3.5 - Biomass

Biomass was estimated using the dry weight of the recovered fish from the mark and recapture study. Because the mark and recapture study only included fish ≥ 40 mm TL, biomass was only estimated for

adult mummichogs. Dry weight was obtained using a wet to dry weight ratio obtained from a subsample of mummichogs. The adult fish collected were then divided into two size classes, 40-54 mm TL and ≥ 55 mm TL, to provide a more accurate estimate of biomass. The size classes were determined based on the recovered fish, as each size class represents ~50% of the recovered fish. A mean dry weight for each size class in each creek was obtained from recaptured fish. Length frequency of the aforementioned size classes was found and applied to the abundance measurements to estimate total biomass of each size class. Biomass was calculated using equation (3), which is similar to Hagan et al., (2007) and Teo and Able (2003) who both also used mummichogs.

$$\text{Eq. (3)} \quad B_{class} = (X_{dw} * A_{class}) / W_A$$

In Eq. (3) B_{class} is the biomass of the specific size class of mummichogs m^{-2} in each creek, X_{dw} is the mean dry weight of the same size class in mg, A_{class} is the abundance of the same size class, and W_A is the Watershed Area of each creek as m^2. The biomass of the 40-54 mm TL and ≥ 55 mm TL size class was then summed to obtain a total adult mummichog biomass from each of the creeks.

Biomass for mummichogs was calculated as mg of dry weight m^{-2} (mg dw m^{-2}) for each creek. A t-test using SAS 9.2 was used to compare the mean biomass estimates among the nutrient-treated (n = 2) and reference creeks (n = 2).

2.3.6 - Secondary Production

Recovered fish from the mark and recapture study were used to estimate secondary production, the population-level change in dry weight over a hypothetical week during the recovery period. Dry weight was obtained from the recovered marked fish in the same manner as mentioned above for the biomass estimates and was based on the length change for each individual. Dry weight was used instead of length to obtain values comparable to traditional secondary production measurements. Secondary production was measured in the same two size classes used to estimate biomass. The mean change in dry weight estimated for a week was obtained for the each size class at each creek. Production was measured for each size class at each creek. Secondary production was calculated using the equation (4), which is similar to Hagan et al., 2007 who also used mummichogs.

$$\text{Eq. (4)} \quad P_{class} = (X_{dw} / \text{Week}) / W_A$$

In Eq. (4) P_{class} is the secondary production of the size class, X_{dw} is the change in dry weight, Week is a hypothetical week, and W_A is the watershed area of each creek as m^2. The production of both size classes was summed to obtain a secondary production estimate in each creek.

Secondary production for adult mummichogs was calculated as milligrams of dry weight m^{-2} (mg dw m^{-2}) for one week for each creek. A t-test using SAS v. 9.2 was used to compare mean secondary production

estimates between the nutrient-treated (n = 2) and reference creeks (n = 2).

2.3.7 - Growth Rates

Growth rates were measured using information gathered from the mark and recapture study from the entire recapture period. To measure individual growth rate, each fish was removed from the freezer and allowed to thaw. Length and weight were measured to the nearest tenth of a millimeter and hundredth of a gram. The coded wire tag was then recovered from the dorsal musculature. The tag number was read using a Magniviewer magnifying tool made by Northwest Marine Technology. This number was compared to the archive where the release date and initial length were found. From this information absolute growth rate was calculated using equation (5), which is similar to Hagan et al., (2007) and Teo and Able (2003) who both also used mummichogs.

$$\text{Eq. (5)} \quad GR = (L_1 - L_0) / (T_1 - T_0)$$

In Eq. (5) GR is the growth rate of each individual fish, L_0 is the initial length, L_1 is the recovered length, T_0 is the Julian date marked, and T_1 is the date recovered.

Growth rate data were analyzed statistically using two different methods: (1) Split-plot ANOVA and (2) curve fitting to a Gompertz growth model. The split-plot mixed model analysis of variance (ANOVA) was conducted in SAS v. 9.2. Nutrient treatment (nutrient enriched and reference) and creek reach (upper and lower) were considered fixed

effects and the creek replication was considered a random effect. For the second method to statistically analyze growth rates, data were fitted to a growth model to test for a difference among the growth coefficient (k) of the model between the treatments. This method eliminates the bias of fish length that may be present if fish size differs among the sampled areas (see Kolmogorov-Smirnov results) since older, larger fish grow slower than younger, smaller fish. Growth data were tested using a model selection process in SAS v. 9.2. Data collected best fit the Gompertz growth model. Von Bertalanffy and logistic growth models were both fitted as well and yielded similar results but with a lower goodness of fit. To test for a statistical difference between nutrient and reach treatments, the 95% confidence intervals of the calculated difference of the growth coefficients (K_{DIFF}) were analyzed for each treatment. If the 95% confidence intervals of K_{DIFF} did not include 0, then a statistically difference to the 0.05 level was concluded. If 0 was included in the 95% confidence interval, the difference could be assumed to be insignificant.

2.3.8 – Density Effects on Growth Rate

Linear regression was used to test for density-dependent effects on growth rate. A standardized growth rate was used rather than actual growth rates to account for age-biased growth. The standardized growth rates were obtained by dividing the growth rates obtained from eq. (5) by the fish length cubed. Length cubed was used

because fish grow three dimensionally and at different rates at different ages and lengths. Growth of mummichogs ≥ 40 mm TL from the flume net samples was used as the independent variable and standardized growth rates from the same creek reaches was used as the dependent variable. All 8 creek reaches were used in this analysis.

2.3.9 – Fulton's Condition Factor

Fulton's condition factor was measured using mummichogs collected for a separate diet analysis independent of the mark and recapture study and flume net samples. Fulton's condition factor can be used as a surrogate of the health of fish. Poorer or lower condition factors can be associated with lower fecundity, slower growth, and larger parasite loads (Ratz and Lloret 2003; Neff and Cargnelli 2004). Fulton's condition factor was calculated using equation (6) (Nash et al. 2006; Mustac and Sinovcic 2010).

$$\text{Eq. (6)} \quad K = (W_g / L_{mm}^3) * 100{,}000$$

In Eq. (6) K is the Fulton's condition factor, W_g is the weight in grams, and L_{mm} is the total length in millimeters.

Fish collected for this analysis were captured using minnow traps on the falling tide during the recapture period. The fish were then placed on dry ice in the field and frozen upon return to the field station. The fish were shipped on dry ice and stored in a -80°C freezer until processing. For analysis, each fish was allowed to thaw, measured to the nearest tenth of millimeter, and wet weighed to

the nearest tenth of a gram similarly to the measurement for mark and recapture study.

A Split Plot mixed model analysis of variance (ANOVA) was used to compare Fulton's condition factor among the TIDE treatments. The nutrient-treatment and the creek-reach treatment were considered fixed effects in the split plot model while the replicates of the creeks were considered a random effect.

2.3.10 – Density Effects on Condition Factor

Linear regression was used to detect density-dependent effects on condition factor. Density of mummichogs ≥ 40 mm TL from the flume net samples were compared to the fish condition among the different creek reaches. Density is the independent variable and Fulton's condition factor the dependent variable. All 8 creek reaches were used in this analysis.

3 - RESULTS

3.1 - Mark and Recapture Numbers

A total of 7841 mummichogs were marked during the mark and recapture study (Table 2). Of these, 214 (2.73%) died before release. After mortalities were accounted for, 7,627 fish were released into the 4 creeks. A total of 3,894 fish were released into reference creeks and a total of 3,733 fish were released into fertilized creeks. Recapture rates varied from 8.5% to 17.1% among the creek reaches and an overall total of 12.8% were recaptured (Table 3). Recaptured fish were usually but not always recovered in the same creek reach where they were released. About 23.7% of the total recaptured fish were recovered in different creek reaches. The nutrient-enriched watershed had higher movement of mummichogs, with 25.2% of the released fish captured on the opposite side of the fish block, compared to 19.0% in the reference creeks. Most fish recovered in a different reach crossed through the fish block (20.0%), while very few moved to the adjacent creek replicate (3.7%).

3.2 - Abundance and Density Measurements

Abundance estimates derived from the mark-recapture study in each creek reach varied from 13,315 to 27,744 individuals, while 95% confidence intervals based on successive recaptures ranged from 3600 to about 8000 in various creek reaches (Table 4). Reference-creek mean densities were 0.59 ± 0.07 (all error terms throughout the text

are standard deviations unless otherwise noted), while fertilized creeks were 0.81 ± 0.04 fish m^{-2} (Figure 3). The difference in mummichog density in the fertilized creeks was 37% higher than reference creeks ($p = 0.055$, $DF = 2$, $t = 4.07$).

Table 2. Number of fish tagged and mortalities each day during the mark and recapture study. All dates are from 2009.

Date	Nutrient Treatment	Rep	Reach Treatment	Fish Tagged	Mortalities	Fish Released	Mortality Percentage
7/7	Reference	1	Upper	531	8	523	1.51%
7/8	Reference	1	Lower	278	1	277	0.36%
7/8	Reference	2	Upper	631	16	615	2.54%
7/9	Reference	1	Lower	560	2	558	0.36%
7/9	Reference	2	Lower	505	2	503	0.40%
7/10	Fertilized	1	Upper	536	6	530	1.12%
7/10	Fertilized	2	Lower	560	5	555	0.89%
7/13	Fertilized	1	Lower	542	24	518	4.43%
7/13	Fertilized	2	Upper	506	8	498	1.58%
7/14	Fertilized	1	Upper	496	31	465	6.25%
7/14	Fertilized	2	Lower	268	2	266	0.75%
7/14	Fertilized	2	Upper	163	0	163	0.00%
7/15	Fertilized	1	Lower	338	0	338	0.00%
7/15	Fertilized	2	Upper	418	18	400	4.31%
7/16	Reference	1	Upper	485	18	467	3.71%
7/16	Reference	1	Lower	271	15	256	5.54%
7/16	Reference	2	Lower	421	21	400	4.99%
7/17	Reference	2	Upper	332	37	295	11.14%
Total				7841	214	7627	2.73%

Table 3. The recapture percentages of each creek reach from mark and recapture study.

Creek	Replicate	Reach Treatment	Recapture Rates
Reference	1	Upper	17.1%
Reference	1	Lower	17.1%
Reference	2	Upper	12.8%
Reference	2	Lower	14.6%
Fertilized	1	Upper	8.7%
Fertilized	1	Lower	8.5%
Fertilized	2	Upper	11.2%
Fertilized	2	Lower	11.7%
		TOTAL	12.8%

Table 4. Abundance estimates and 95% confidence intervals of each creek reach derived from mark and recapture study.

Creek	Rep	Reach Treatment	Abundance	95% Confidence Intervals
Reference	1	Upper	13,315	8,576 – 18,054
Reference	1	Lower	17,371	12,552 – 22,190
Reference	2	Upper	22,069	16,674 – 27,464
Reference	2	Lower	14,196	10,569 – 17,823
Fertilized	1	Upper	No Measurement	No Measurement
Fertilized	1	Lower	27,113	19,302 – 34,924
Fertilized	2	Upper	27,744	21,255 – 34,233
Fertilized	2	Lower	25,398	17,006 – 33,790

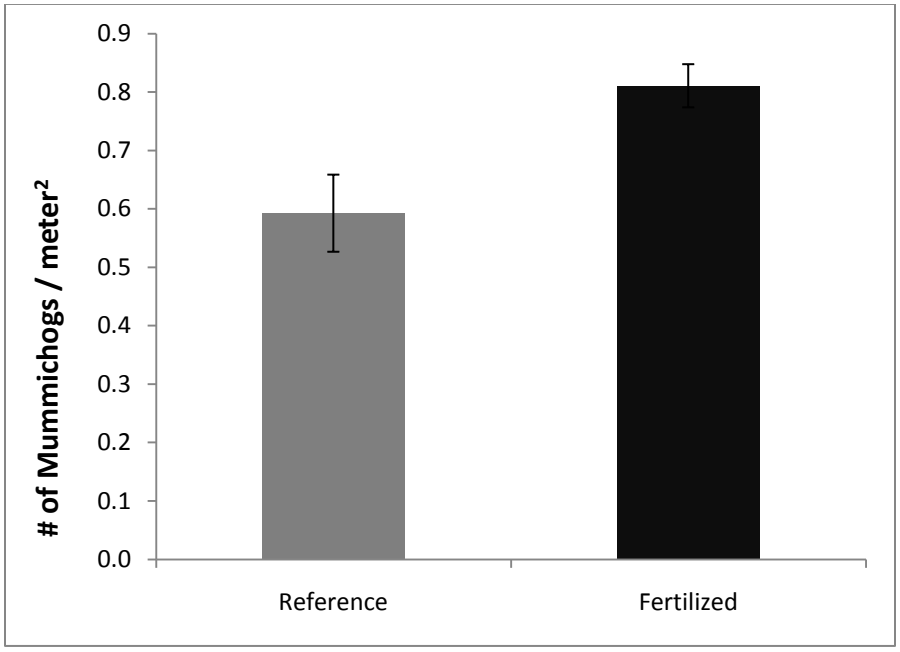

Figure 3. Density of mummichogs (X ± Standard Deviations (SD)) at reference (n = 2) and fertilized (n =2) creeks estimated from the mark and recapture study. Density is expressed as mean mummichogs ≥ 40 mm per m^2.

Flume net derived estimates of adult mummichog (≥ 40 mm TL) density in fertilized creeks were 0.35 ± 0.16 compared to 0.15 ± 0.14 adult mummichogs m^{-2} in reference creeks (Figure 4), but were not

significantly different ($F_{1,2}$ = 3.76, p = 0.19), likely due to the high variability among the two replicates located at each creek reach. The creek-reach treatments were not significant ($F_{1,10}$ = 0.00, p = 1.00) with virtually identical means in lower and upper reaches (0.25 ± 0.19 and 0.25 ± 0.18 adult mummichogs m^{-2}, respectively). There was also no interaction between nutrient enrichment and reach ($F_{1,10}$ = 0.00, p = 1.00).

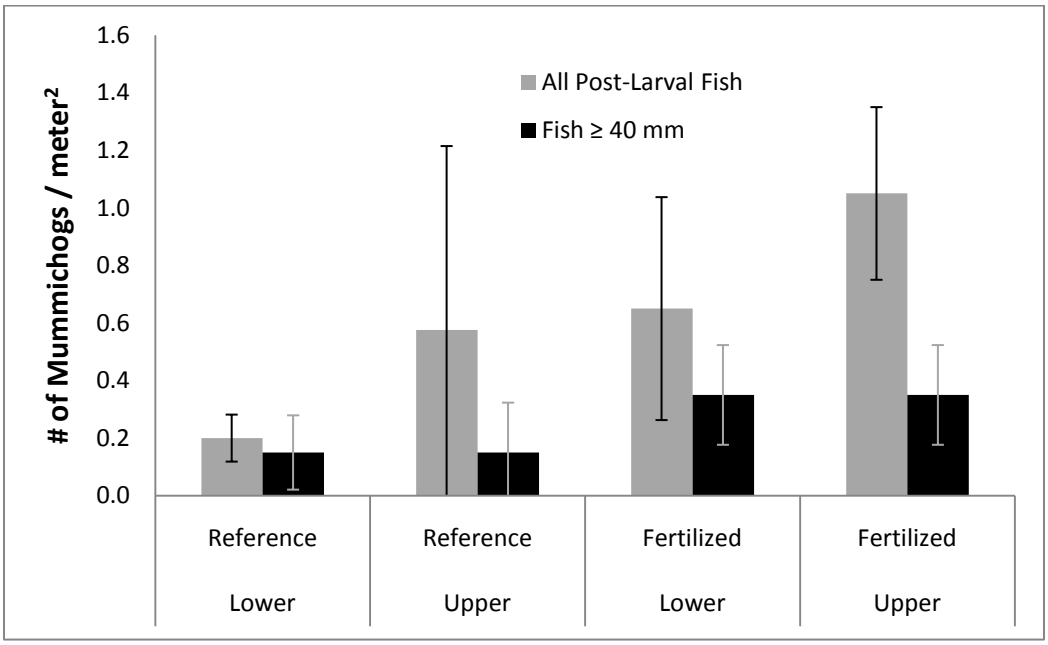

Figure 4. Density of mummichogs (X ± SD) at reference (n = 2) and fertilized (n = 2) creeks as well as Lower (n = 2) and Upper (n = 2) reaches measured from flume net samples. Density is expressed as mean post-larval mummichogs (> 15 mm) and mummichogs ≥ 40 mm per m^2.

Flume net derived density estimates of all post-larval (≥ 15 mm TL) mummichogs were 0.39 ± 0.47 mummichogs m^{-2} in reference compared to 0.85 ± 0.39 mummichogs m^{-2} in fertilized creeks. This difference was not significant ($F_{1,2}$ = 4.06, p = 0.18), likely because of the high

variability among replicates. The creek reach treatment was not significant ($F_{1,10}$ = 3.88, p = 0.08) with 0.81 ± 0.53 mummichogs m^{-2} in the lower reach and 0.43 ± 0.35 mummichogs m^{-2} in the upper reach. There was also no interaction ($F_{1,10}$ = 0.00, p = 0.95).

3.3 - Measurement Correlation

Abundance of mummichogs estimated from the mark-recapture study followed similar trends compared to that estimated by flume nets for adult mummichogs among the creek reaches (Figure 5). Correlation analysis determined the relationship was significant at the 0.055 level (Correlation coefficient = 0.71).

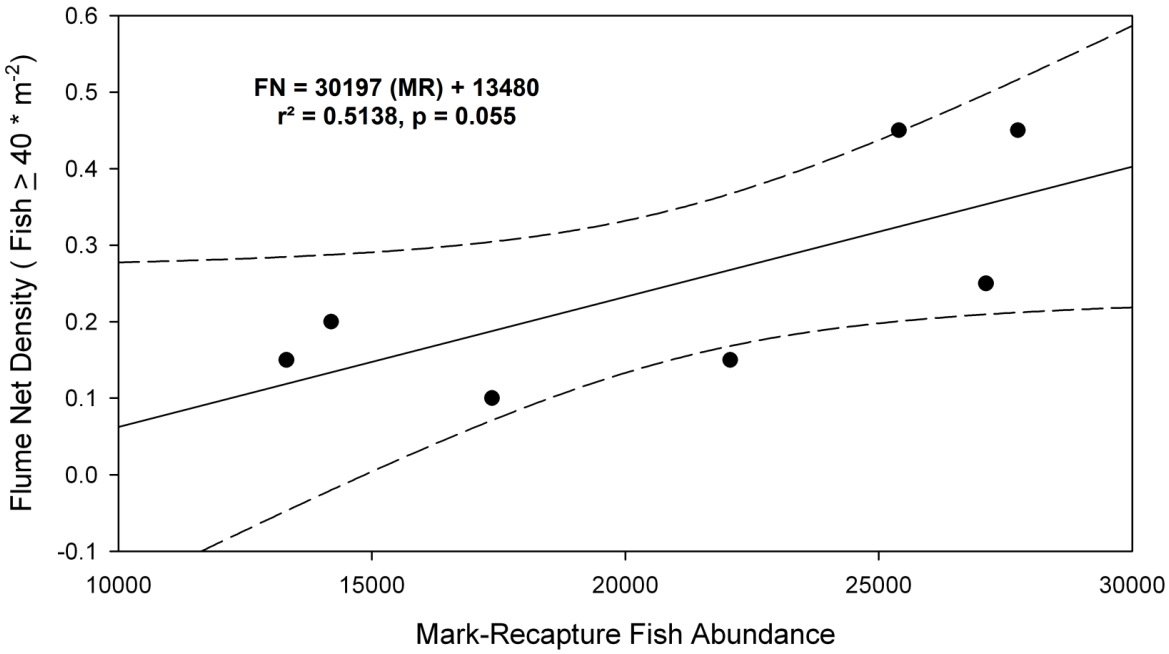

Figure 5. Correlation of mark and recapture abundance and flume net density of mummichogs ≥ 40 mm. The solid line is the best fit line and the dotted lines are the 95% confidence intervals.

3.4 - Length Distribution

Mummichogs in reference creeks had a mean length of 55.3 ± 10.9 mm TL and median length of 52 mm TL. Fish in fertilized creeks had a mean length of 58.4 ± 10.2 mm TL and median length of 56 mm TL. The Kolmogrov-Smirnov test indicated that the distributions were significantly different (Figure 6, Ksa = 8.97, $p < 0.001$) with mummichogs in the nutrient-enriched creeks being larger on average in both mean and medians.

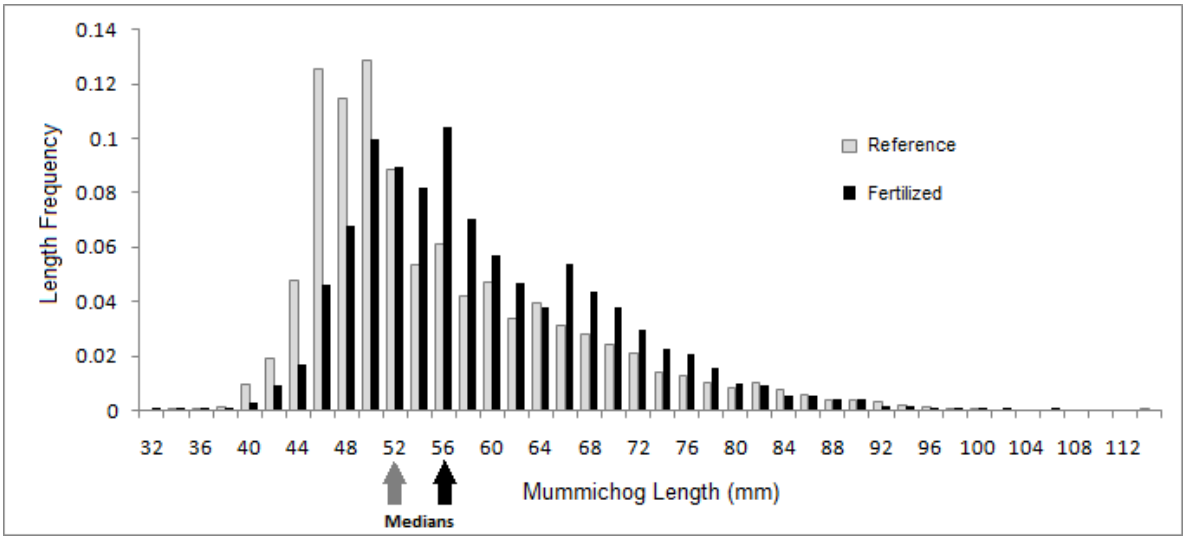

Figure 6. Body size distributions of reference (n = 4,003) and fertilized (n = 3,825) marked fish. The arrows represent the medians of the reference and fertilized creeks.

3.5 - Biomass

Reference creeks yielded mean biomass estimates of 338.5 ± 26.7 mg dw m^{-2} and fertilized creeks had biomass estimates of 522.9 ± 36.1 mg dw m^{-2} (Figure 7). Mummichog biomass was significantly higher in fertilized creeks (DF = 2, t = 5.81, p = 0.028).

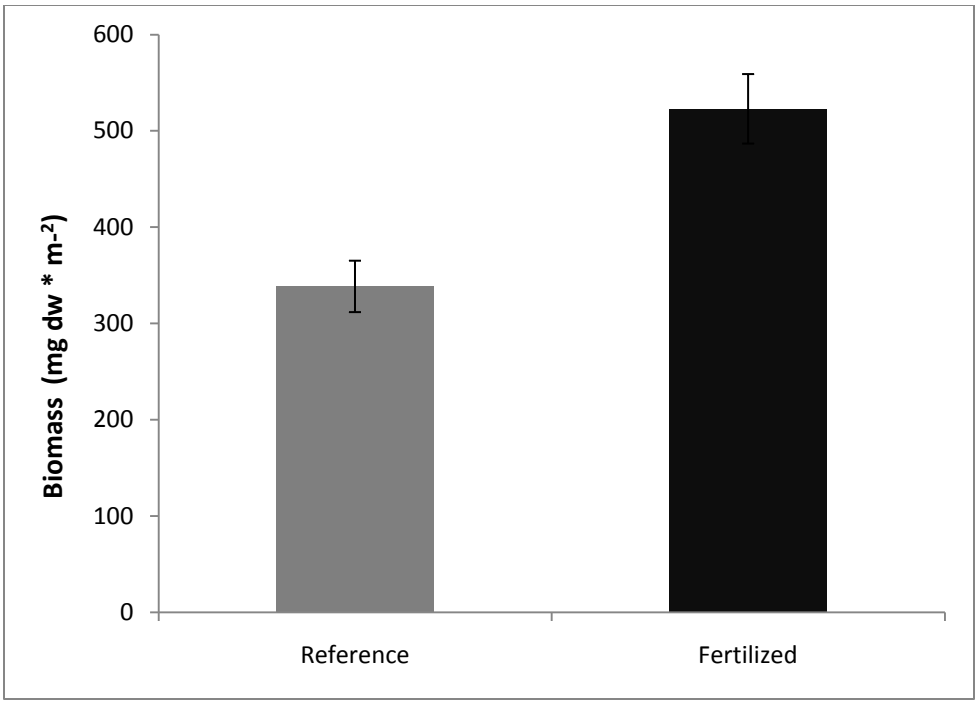

Figure 7. Biomass estimates (X ± SD) of reference (n = 2) and fertilized (n = 2) creeks. Biomass measurements are expressed as milligrams of dry weight per meter squared.

3.6 - Secondary Production

Reference creeks had secondary production estimates of 9.9 ± 1.4 mg dw m^{-2} and fertilized creeks had secondary production estimates of 10.9 ± 1.3 mg dw m^{-2} for one week (Figure 8). This secondary production difference was not significant (DF = 2, t = 0.71, p = 0.552).

3.7 - Growth Rate Analysis

A total of 710 mummichogs were included in the split plot ANOVA test for growth-rate variation. Mean growth rates were 0.102 ± 0.089 mm d^{-1} for the reference creeks and 0.069 ± 0.066 mm d^{-1} for fertilized creeks (Figure 9). This difference was significant at the 0.05 level ($F_{1,2}$ = 23.44, p = 0.040). The mean growth rates for the reaches were

0.096 ± 0.079 mm d^{-1} for the lower reach and 0.085 ± 0.087 mm d^{-1} for the upper reach (Figure 10). This difference was not significant at the 0.05 level ($F_{1,704}$ = 0.90, p = 0.343). There was also no interaction among the treatments ($F_{1,704}$ = 0.00, p = 0.950). Growth rate was strongly but inversely related to initial size for mummichogs in the mark and recapture study (Figure 11, p < 0.001); therefore an analysis to remove length bias was used.

A total of 902 mummichogs were analyzed and fitted to a Gompertz growth model. Reference creeks had a growth coefficient of 0.0041 ± 0.0003 and fertilized creeks had a growth coefficient of 0.0029 ± 0.0004. The calculated difference, K_{DIFF} (= 0.0012), had 95% asymptotic confidence intervals that did not include 0 (-0.0021, -0.0005); therefore, I conclude that the growth coefficients of the two treatments were different, with fish from reference creeks having faster growth.

Fewer mummichogs (710) were analyzed to test for a reach effect because fish that moved across the fish block were removed from analysis. These data were also fit to a Gompertz growth model. The lower reach had a growth coefficient of 0.0040 ± 0.0003 and the upper reach had a growth coefficient of 0.0035 ± 0.0005. The asymptotic 95 % confidence intervals of K_{DIFF} (= 0.0005) included 0 (-0.0014, 0.0004); therefore, I concluded growth rate was unaffected by reach.

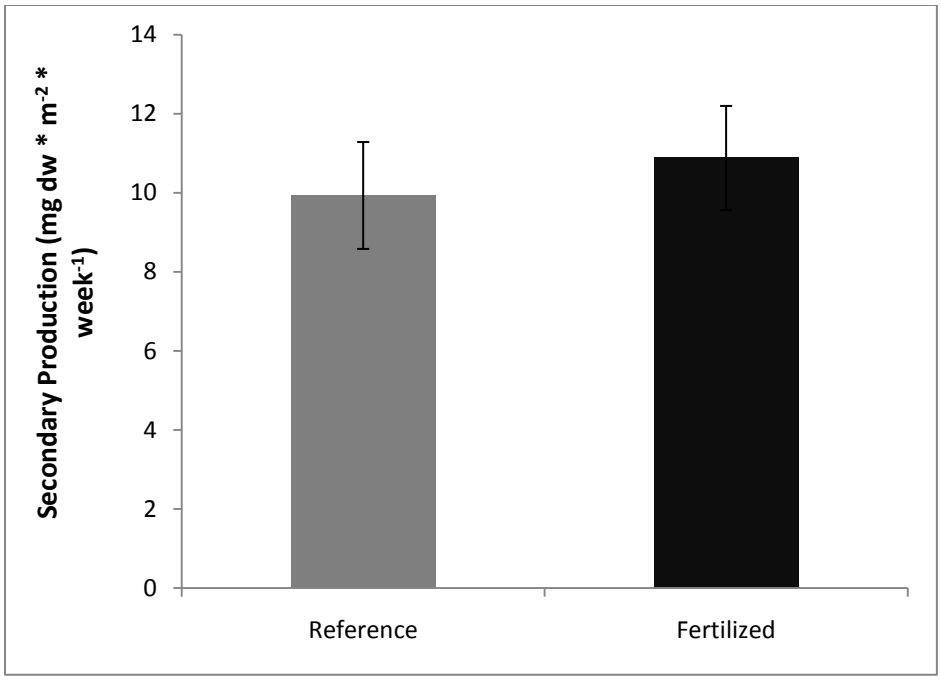

Figure 8. Secondary production estimates (X ± SD) of reference (n = 2) and fertilized (n = 2) creeks. Secondary production measurements are expressed as milligrams of dry weight per meter squared over a hypothetical one week period during the recapture portion of the mark and recapture study.

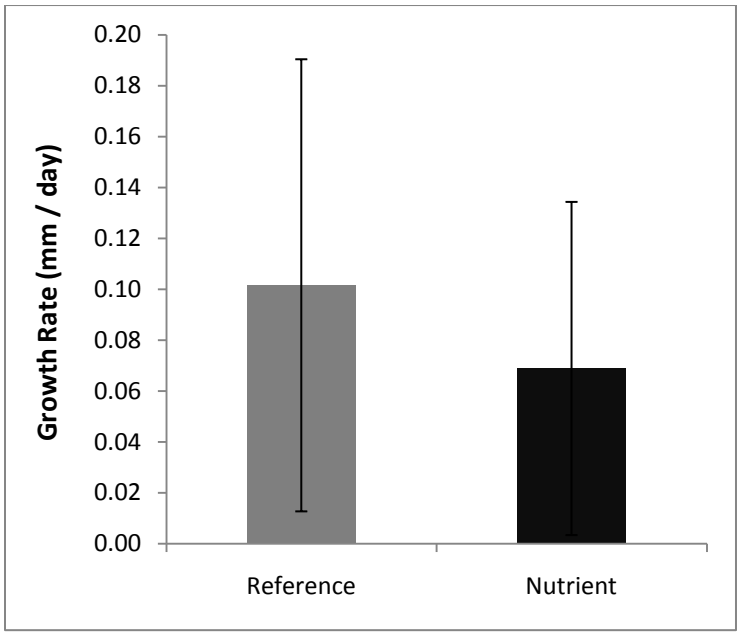

Figure 9. Mean growth rate estimates (X ± SD) of reference (n = 461) and fertilized (n = 249) creeks. Growth rates are expressed as mm of growth per day.

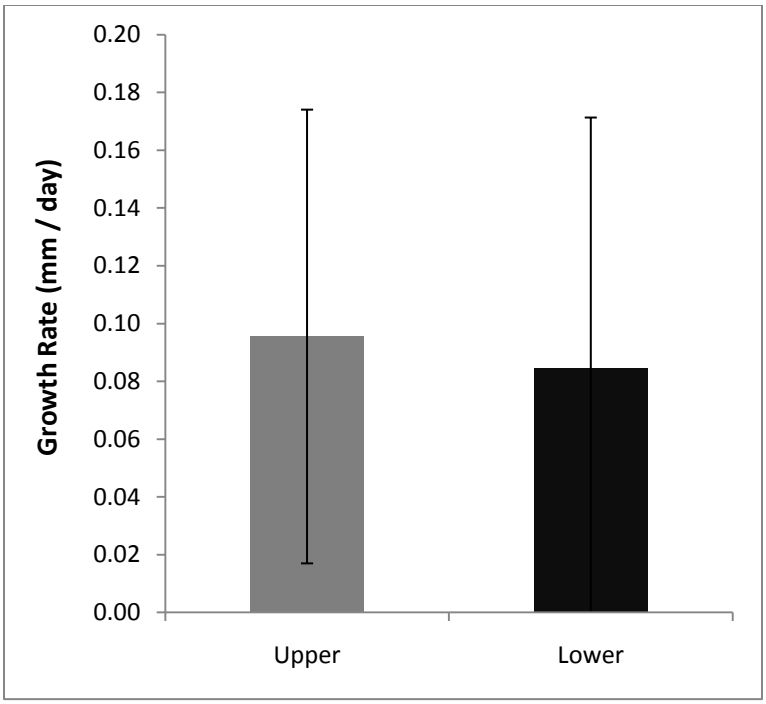

Figure 10. Growth rate estimates (X ± SD) of Lower reach (n = 350) and Upper (n = 360) creeks. Growth rates are expressed as mm of growth per day.

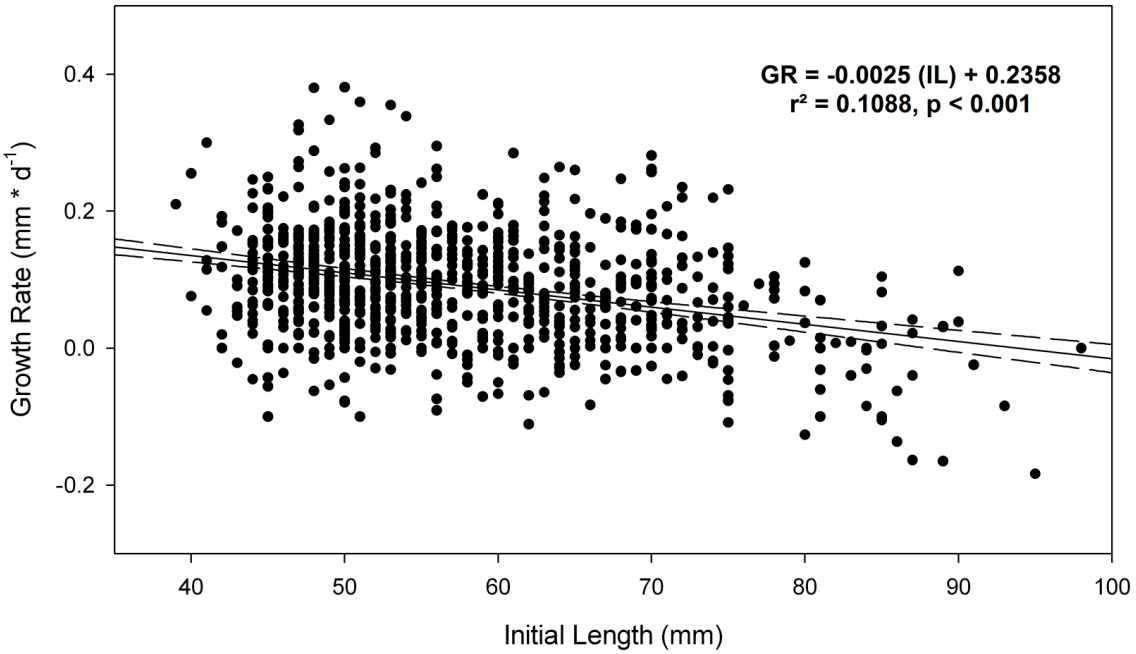

Figure 11. Linear regression of initial length of marked mummichogs (n = 910) effects on growth rates. The solid line is the best fit line and the dotted lines are the 95% confidence intervals.

3.8 - Density Effects on Growth Rate

Standardized growth rate decreased as density of adult mummichogs estimated by flume net increased among the 8 creek reaches (Figure 12). This regression was significant at the 0.05 level (DF = 7, R^2 = 0.79, p = 0.003).

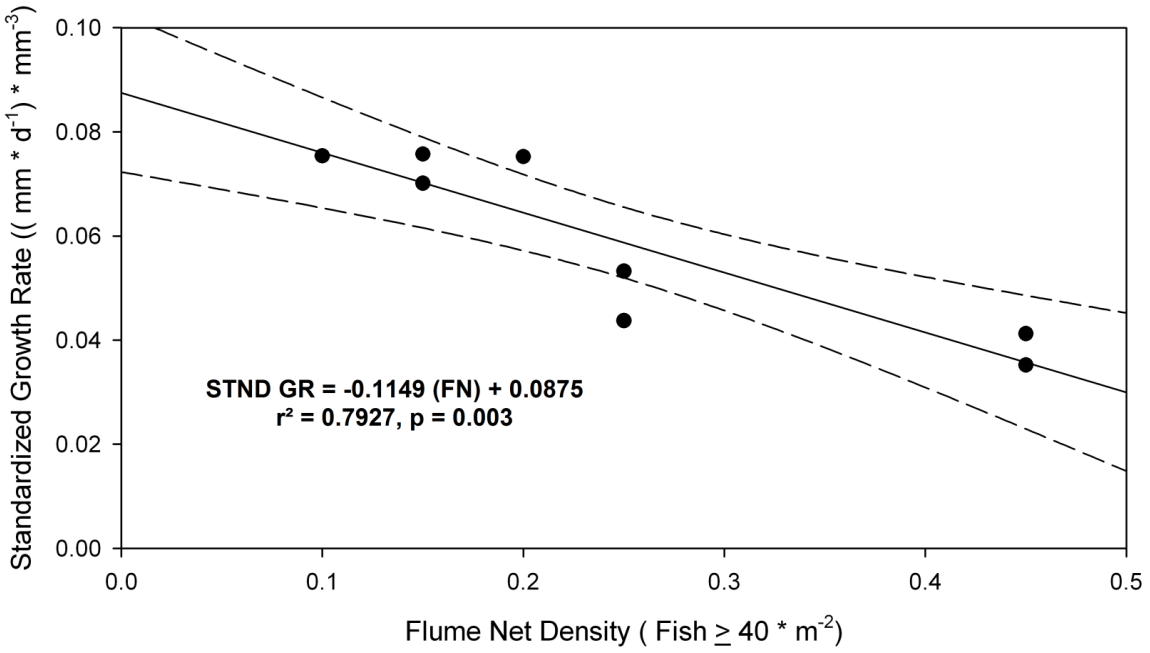

Figure 12. Linear regression (n = 8) of flume net density for fish ≥ 40 mm effects on standardized growth rates. Standardized growth rates are equal to the mm per day divided by length cubed. This measurement accounts for length bias. All 8 creek reaches were used. The solid line is the best fit line and the dotted lines are the 95% confidence intervals.

3.9 - Fulton's Condition Factor

The mean Fulton's condition factor was 1.3 ± 0.19 across all samples. Higher values should indicate a plumper, healthier fish. Split-plot ANOVA revealed no nutrient effect ($F_{1,2}$ = 2.41, p = 0.261), reach effect ($F_{1,356}$ = 0.26, p = 0.613), or nutrient by reach

interaction ($F_{1,356}$ = 0.24, p = 0.843). Reference creeks had a mean Fulton's condition factor of 1.32 ± 0.23 and fertilized creeks had a similar value of 1.27 ± 0.13 (Figure 13).

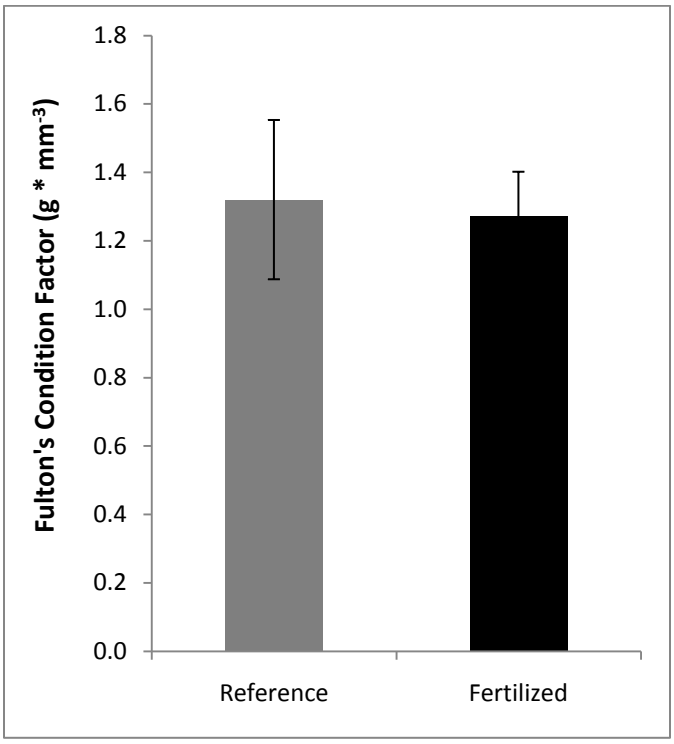

Figure 13. Fulton's condition factor estimates (X ± SD) of reference (n = 185) and fertilized (n = 177) creeks. Fulton's condition factor measurements are expressed as weight (g) divided by length (mm) cubed.

3.10 – Density Effects on Condition Factor

Fulton's condition factor did not vary with density of adult mummichogs estimated by flume nets (DF = 7, R^2 = 0.23, p = 0.22, Figure 14). This suggests that Fulton's condition factor did not vary in a density-dependent fashion among the 8 creek reaches. Fulton's condition factor also did not vary with all post-larval mummichog (≥ 15 mm TL) density estimated by flume net (DF = 7, R^2 = 0.33, p = 0.13).

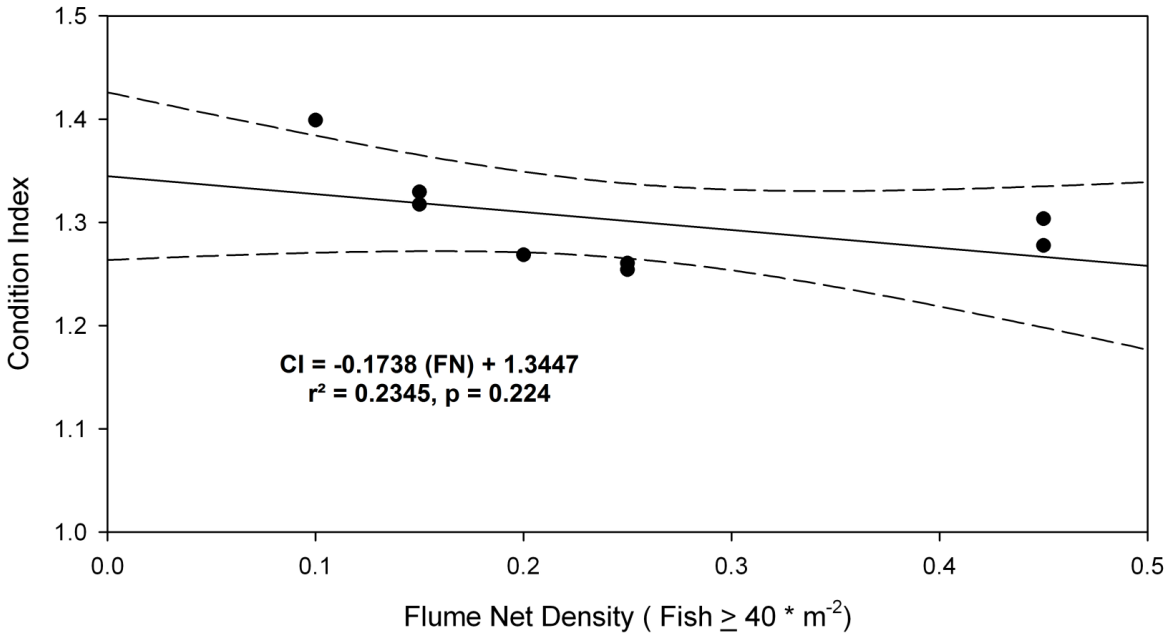

Figure 14. Regression (n = 8) of flume net density for fish ≥ 40 mm effects on Fulton's condition factor. All 8 creek reaches were used. The solid line is the best fit line and the dotted lines are the 95% confidence intervals.

4 - DISCUSSION

4.1 – Summary

My results suggest that nutrient enrichment affected the mummichog population in Plum Island Estuary (PIE) salt marshes. Mummichogs in creeks with nutrient enrichment were significantly larger in body size and biomass but experienced decreased growth rates in mid-summer collections. Mummichogs in nutrient-enriched creeks were 37% more abundant, although the difference was only marginally significant statistically. There was no evidence for nutrient enrichment effects on secondary production or Fulton's condition factor during the period of study. However, increasing densities of mummichogs had a negative effect on mummichog growth rate, but there was no evidence that density affected Fulton's condition factor. These observations suggest that the response of mummichogs to nutrient enrichment may vary over time (e.g., growth rates or secondary production may vary seasonally with nutrient enrichment) because at the time of my study larger fish were present in the fertilized creeks, but growth rates were reduced by nutrient enrichment in these same creeks. These observations also suggest that the increase in density associated with nutrient enrichment may induce density-dependent responses in mummichogs. These findings also suggest that predation pressure associated with higher mummichog abundance and biomass in the nutrient-enriched creeks could increase top-down

control by mummichogs on marsh-dwelling benthic algae and invertebrates.

The overall larger body size and biomass of mummichogs in the fertilized creeks may be attributed to bottom-up effects associated with 6 years of nutrient enrichment. The added nitrogen and phosphorous likely stimulated the benthic algae which in turn stimulated benthic invertebrates (Posey et al. 1999; Posey et al. 2002; Cain et al. 2008). Both benthic algae and benthic invertebrates are known food sources for mummichogs (Allen et al. 1994). The increased quantity of food resources may also have a higher food quality. Johnson and Fleeger (2009) found that the nutrient enrichment in PIE led to an increase in the biomass and body size of some benthic infaunal invertebrates that serve as prey to mummichogs. Recent studies (Johnson, in press) in PIE also found nutrient enrichment stimulated the abundance and biomass of epifauna (amphipods, isopods, and small snails), which mummichogs prey upon on the marsh platform. Also in PIE, Deegan et al. (2007) found that benthic algae increased in treatments with the combination of nutrient enrichment and reduced mummichog abundance. The increases in benthic algae may also elevate grazing rates and food quantity or quality. Other investigators have suggested that herbivorous fish may be regulated by bottom-up factors (Flecker et al. 2002). Several studies have examined top-down and bottom-up factors in estuarine settings

(Posey et al. 1999; Posey et al. 2006); however, no previous studies have experimentally examined bottom-up effects on salt-marsh fishes in the same manner as TIDE.

4.2 – Results Interpreted

4.2.1 - Mortality, Recapture Rates, and Movement

The marking-related mortality rate in this experiment was lower than a previously performed study with mummichogs using coded wire tags and generally similar methods (Hagan et al. 2007). This low mortality rate was expected, especially with the larger size class of fish used in my experiment. Recapture rates varied considerably among the treatment areas and from reach to reach.

Recapture rates were higher in the reference creeks, most likely due to easier access and simpler landscapes (including fewer ditches, intertidal pools and pannes) found there (Deegan, personal communication). Kneib (2009) also found higher mummichog recapture rates associated with simpler marsh landscapes. More fish were present in the fertilized creeks, which could also explain the lower recapture rate. If the overall effort put forth to recapture fish was equal in both reference and fertilized creeks, fewer marked fish should be recovered where more fish are present. The overall recapture rate is similar to other mummichog studies in Atlantic coast salt marshes using similar methods (Hagan et al. 2007; Kneib 2009). In these studies recapture rates were also highly variable from site

to site peaking around 15% after a similar duration (first ~70 days of study) of this study.

Only 33 of the 902 marked recaptured mummichogs in this study relocated into adjacent creeks (between 150-600 m apart). Adult mummichogs (≥ 40 mm TL) exhibited high site fidelity and generally do not relocate to different watersheds (Hagan et al. 2007); therefore, the low percentage relocating into adjacent creeks is expected. Able et al. (2006) found mean mummichog movements of most of the fish to be less than 30 m without variation due to body size. However, my results indicate that about 20% of the fish released in one creek reach moved to the adjacent reach in the same creek during the 2-week recapture period. There was no observable pattern to fish movement (i.e., fish did not show a preference for movement towards upper or lower reaches nor did movement appear to be in response to high fish density). Entire creeks in my study span 230-335 m in distance, with distances among creek reaches ranging from 0-200 m, suggesting that fish in PIE disperse frequently but for only relatively short distances. Movement across reaches was unaffected by the nutrient treatment.

4.2.2 - Abundance and Density Measurements

The density of large mummichogs (≥ 40 mm TL) estimated from the mark and recapture study was more than twice that of the density estimated from the flume net samples. Despite these differences, the

flume net estimates were well correlated with mark-recapture results among the creek reaches ($r = 0.71$, $p = 0.06$). Fish density is rarely estimated by independent and complementary techniques in large, open settings such as a salt marsh. The correlation between densities calculated from the mark-recapture and flume net methods suggests that my estimates of fish density used to determine density-dependent effects on growth rate and condition factor were accurate and justified (see below). Mummichogs are known to enter the intertidal marsh surface to feed during spring high tides (MacKenzie and Dionne 2008). Amphipods and terrestrial insects are frequently found in mummichog gut contents further suggesting feeding on the marsh platform (Allen et al. 1994). The mark and recapture estimates of density should be higher than flume net estimates. This happens because the mark and recapture estimates includes all large mummichogs in the sub-tidal creek, ditches and pannes, whereas flume net estimates only measure mummichogs utilizing the marsh platform. All fish in the creek should not be expected to use the marsh platform at any given time. Based on these estimates, 25.4% of the fish at reference sites and 43.2% of the fish at nutrient-enriched sites move up on the intertidal marsh platform at high tide. The higher proportion moving onto the flooded marsh platform in the nutrient-enriched creeks could be due to increased food sources available on the marsh platform. Johnson (in press) found that the densities of

intertidal epifauna (amphipods, isopods, and small snails) were higher after multiple years of fertilization.

The density measurements from this experiment are slightly lower compared to other studies of mummichogs in salt marshes. One study conducted in southern New Jersey in Delaware Bay found mummichog densities of large fish to be 1.7 fish m^{-2} and 20.2 fish m^{-2} for the smaller size class (Hagan et al. 2007). This was a similarly conducted mark and recapture study in a *Spartina* sp. dominated marsh using identical size classes and conducted during the summer months. Another similar study also conducted in Delaware Bay measured annual population density of mummichogs $\geq$ 30 mm TL to be 1.2 fish m^{-2} with densities peaking at 2.9 fish m^{-2} in the late summer (Teo and Able 2003). Young sub-adult mummichogs (< 30 mm TL) were found at densities of 15.1 fish m^{-2} and peaking at 41.4 fish m^{-2}. These size classes are not directly comparable to my experiment which could contribute to the density difference. Another reason for the apparent lower densities in PIE could be that the other studied marshes are located further south than Plum Island Sound, Massachusetts. A marsh in Delaware Bay would experience warmer temperatures for longer periods of time than the Massachusetts marsh used in this experiment stimulating higher growth (Hedeholm et al. 2011).

Although both mark-recapture and flume net estimates of fish density were higher (a 37% increase based on mark-recapture and 133%

increase based on flume net data) in nutrient-enriched creeks, neither estimate was statistically significant at the 0.05 level. Variability was high in the flume net study and sample size was low in the mark-recapture study due to the design, despite the large amount of fish marked. Nevertheless these findings should be considered biologically significant because the large consistent increase in abundance (pre-nutrient-enrichment, 2003, mummichog densities were not statistically different, Deegan et al. 2007) contributed to significantly higher fish biomass in nutrient-enriched creeks and because abundance affected mummichog growth rate.

4.2.3 - Size Distribution

Length-frequency distribution patterns were similar in both nutrient and reference creeks; however, central tendencies estimated by mean and median differed. Fish in the nutrient creeks were larger, by a mean of 3 mm and a median of 4 mm than fish in the reference creeks. Growth rate data (see below) do not suggest that the fish in the fertilized creeks were growing at a faster rate at the time of the study. If differences in growth rate were responsible for the variation in size frequency distribution, it is possible fish in nutrient-enriched creeks may have began the season larger from previous years' nutrient enrichment or may have grown faster earlier in time before growth-rate measurements were taken. At the time of measurements in early July, the mummichogs were well into both the

growing season and the nutrient-enrichment regime. Other factors like predator selection may also influence size-frequency distributions. Striped bass and avian predators are present in and around the Rowley River (Kneib 1982; Pautzke et al. 2010) and may exhibit size selection on the mummichog population by consuming more small fish in the nutrient-enriched creeks.

4.2.4 - Biomass

The biomasses of large mummichogs in this experiment were lower than that found in other experiments conducted under similar conditions. Biomass for adult mummichogs was estimated in two southern Delaware Bay studies to be 1,250 mg dw m^{-2} (Hagan et al. 2007) and 879.1 mg dw m^{-2} (Teo and Able 2003) during the same time of the year (July & August) that my study was conducted. This higher biomass in these other experiments could reflect the geographical locations allowing for different abundances and growth (Schultz et al. 1996; Hedeholm et al. 2011). Nutrient-enriched creeks had 54.4% higher biomass than reference creeks in PIE. This was significant ($p = 0.028$) and likely due to bottom-up effects as described previously.

4.2.5 - Secondary Production

The estimated secondary production values from this experiment are lower when compared to other similar studies. Studies of large mummichog secondary production during the summer months ranged from 85.2 to 161 mg dw m^{-2} $week^{-1}$ (Teo and Able 2003; Hagan et al. 2007). The

lower values in PIE are likely due to the cumulative effects of the lower densities, lower biomass, and slower growth associated with my study. The geographical location may explain the higher production as all previous studies dealing with densities, biomass, and growth were conducted south of Massachusetts where these values should be higher due to longer growing seasons and higher temperatures (Schultz et al. 1996; Hedeholm et al. 2011).

Secondary production varies with changes in abundance and biomass as well as growth. While nutrient-enriched creeks had higher abundance and biomass, fish in reference creeks were growing faster during the study periods. The two measurements counteracted each other and reduced the difference between reference and fertilized creeks' secondary production.

4.2.6 - Growth Rates

Mummichog growth rates in my experiment in PIE were on the lower range of similarly done mark and recapture experiments with mummichogs. In a similar study (Kneib 2009) in Georgia using large mummichogs, growth rates ranged from 0.099 mm d^{-1} to 0.274 mm d^{-1}. In another experiment (Hagan et al. 2007) in Delaware Bay, growth rates of large mummichogs in *Spartina* marshes ranged 0.09-0.37 mm d^{-1} with an mean of 0.24 mm d^{-1} (Hagan et al. 2007). This experiment grouped fish > 35 mm TL with large fish which could explain the slightly higher mean. In another experiment (Teo and Able 2003) in Delaware Bay,

growth in early summer months (June-July) was 0.28 mm d^{-1} for all size classes. The slower growth rates in my experiment could reflect geographical location as all these experiments were conducted south of Massachusetts and have longer growing seasons and higher temperatures (Schultz et al. 1996; Hedeholm et al. 2011). Slightly different size classes could also explain some differences since young mummichogs ($\leq$ 40 mm TL) growth rates are generally much higher than larger mummichogs (0.44 mm d^{-1}, Able et al. 2006).

Growth rates in PIE were 47.8% higher in reference creeks than nutrient-enriched creeks, despite density and biomass both being greater in the nutrient-enriched creeks. It is possible that the difference in mummichog body size among creeks contributed to differences in growth rate. As consistent with most fish species, smaller mummichogs grow at much faster rates than larger mummichogs (Able et al. 2006). Because a higher percentage of larger fish were present in fertilized creeks, a statistical analysis removing length bias was performed. However, after fitting data to a Gompertz growth model which fits the entire population's growth rate from each treatment, growth rates in the reference creek were also found to be greater than in nutrient-enriched creeks. From this analysis I can conclude that the growth rates were different even when taking a size bias into account.

Density-dependent effects via intraspecific competition may have caused lower growth rates in nutrient-enriched creeks where abundance and biomass of fish were increased. Fish were present in higher biomasses in fertilized creeks which could lead to competition for food and space (Cross and Stiven 1999). Growth rates could slow in the nutrient-enriched creeks if the negative effects of increased competition from higher density and biomass outweighed the positive effects of nutrient enrichment on resource quantity and quality. Further evidence that growth rates slowed due to high abundance was evident as standardized growth rate significantly decreased with increasing mummichog density (Figure 12). The regression further suggests density-dependent effects on growth rates among the mummichog populations in PIE.

An alternative explanation associated with density-dependent effects for reduced growth rates could be that fish prey may shelter more frequently when predator abundance increases (Werner and Hall 1974). Large mummichogs are known to prey on smaller mummichogs (Able et al. 2007). If small mummichogs sense the increased abundance of large mummichogs, they may seek shelter more frequently and reduce foraging time. The result could be a slower growth rate at higher mummichog density. Additionally, Johnson et al. (2009) found that the incidence of parasitism of amphipods was increased in nutrient-enriched creeks in PIE. *Fundulus* has many parasites (Harris and

Vogelbein 2006), and if the same effect of nutrient enrichment occurs with mummichog parasites, the increased parasite load could be associated with reduced growth rates.

There was no evidence of a reach effect on body size from either the ANOVA growth rate analysis or Gompertz growth model analysis. Landscape effects of upper and lower creek reaches did not influence mummichog growth rate.

4.2.7 - Fulton's Condition Factor

Higher condition factor values are associated with healthier fish (Nash et al. 2006), and means in PIE were similar to or higher than other studies with mummichogs. In a laboratory experiment, mummichogs condition factors ranged from 1.05-1.15 (Martel et al. 2010). In a field study in July, condition factors ranged from 1.14-1.33 for mummichogs in New Brunswick, Canada (McMullin et al. 2009). These data suggest that mummichogs in PIE were very healthy in both reference and fertilized creeks at the time of my study.

There was no evidence that nutrient enrichment affected Fulton's condition factor. Condition factor was slightly higher in reference creeks, but not statistically different, even though growth rates declined in the same creeks. If increased intraspecific competition was occurring in nutrient-enriched creeks with higher densities as the growth rate data suggests, an expected result would be lower fish condition. This would be caused by reduced food resources per

individual and more stress associated with more competing mummichogs in these creeks. Nevertheless, fish density did not affect condition factor (Figure 14). Growth rates were greater in reference creeks also suggesting fish should be healthier in these reference creeks. The maximum condition factor for mummichogs is not known, but it could be that the mummichogs in PIE are growing near optimum in all creeks and the condition factor may not be sensitive enough to observe a difference, especially at the high values observed. It is also possible that condition factor is not effective in measuring condition over the short term (i.e., two weeks) because the index measures factors (weight and length) that change slowly, even under severe conditions. A 7-day study conducted on mummichogs exposed to toxins found no significant differences among treatments suggesting longer response times might be required to measure changes in condition (Martel et al. 2010).

There was also no evidence for a creek-reach treatment effect on Fulton's condition factor. This is not surprising since growth rate also did not vary with the creek-reach treatment. The lack of evidence suggests that the upper and lower creek reach do not influence fish condition.

4.3 – Questions Answered

4.3.1 – Question (1) - "Does Nutrient Enrichment Effect the Mummichog Population in PIE?"

The answer to my overarching question is that the 6 years of

nutrient enrichment had a net positive effect on the mummichog population in PIE. Nutrient enrichment marginally increased abundance and significantly increased biomass, which are known possible short-term effects of nutrient enrichment in the absence of hypoxia (Nixon and Buckley 2002), but with no decrease in mummichog condition factor. This experiment was conducted in Massachusetts which experiences large diurnal tidal cycles. Tide heights reach 3-4 m which consistently circulates the sea water that flows in and out of local marshes. Because of this circulation, hypoxia caused by eutrophication with nutrient enrichment should not occur in PIE intertidal and sub-tidal creeks; therefore, negative effects associated with hypoxia were most likely not occurring.

It remains to be seen how continued nutrient enrichment will influence mummichogs. Negative effects could come in the form of an increasing population density of mummichogs increasing the magnitude of the density-dependent effects, especially if population size increases at a greater rate than resources stimulated by nutrient enrichment. Observed growth rate reductions in the nutrient-enriched creek suggest this may have already occurred. Mummichog growth rate decreased with increasing density in the creek reaches. While more food was likely available, it is possible that mummichogs reached abundances at which even the added food could not maintain the larger population, slowing individual growth. Population increases in

nutrient-enriched creeks of 37% may have been sufficient to induce density-dependent effects. One other possibility for decreased growth rates is the mummichogs did not directly benefit from the increase in primary production. Large snails, *Ilyanassa obsolete*, in the creek channel experienced a 4 fold increase in abundance under nutrient enrichment (Johnson and Short, in preparation) and therefore graze more benthic algae in nutrient-enriched creeks (Pascal et al., in preparation). Large snails are not consumed by mummichogs; therefore, mummichogs would not benefit from the increased production, preventing classic bottom-up production of the mummichog population. Other grazers are found in PIE marshes (e.g., amphipods, grass shrimp) that may reduce the overall short and long-term bottom-up effects of nutrient enrichment on the mummichogs (Hillebrand 2002) by outcompeting fish for benthic algae, especially if herbivory contributes significantly to density and biomass increases in mummichogs.

4.3.2 - Question (2) - "Does Abundance Affect Mummichog Growth Rate and/or Health?"

Mummichog abundance affected growth rate but did not affect condition factor. As abundance increases, density-dependent effects may induce intraspecific competition or behavioral changes that affect growth rate. Health via Fulton's condition factor estimates did not vary with mummichog density and were equivalent in the reference and nutrient-enriched creeks. Condition factor may not be an adequate

measure of health in the short term for the mummichog. While growth rate changes were detected, condition changes may take more time to manifest or become detectable. Furthermore, mummichogs in PIE appear very healthy in all creeks and among all treatments.

4.3.3 - Question (3) - "Does Landscape Type Affect Mummichog Growth Rate and/or Health?"

No differences were found in growth rates or condition of mummichogs in the upper and lower reaches of the first order creeks studied. Creeks are shallower and narrower in the upper reach. The lower reaches retained more water with a deeper creek channel leaving the upper reaches air-exposed for longer periods of time. Kneib (2009) found growth rates of mummichogs to be highest in simple landscape conditions (i.e., less tidal channel edge within an area and fewer creeks and ditches). Landscape differences between upper and lower reaches in PIE may be less than in Kneib's study. Upper and lower reaches in my experiment were simply arbitrary point where a creek was divided, whereas Kneib measured an actual complexity value. This question remains currently unanswered in PIE.

4.4 – Future Studies

Based on the results and analysis obtained from my thesis work, future studies could be better designed to address several unresolved questions. First, measurements throughout the seasons should be conducted to find if temporal variation in mummichog condition factor occurs with nutrient enrichment. As stated above, the two week period

in this experiment may not have been of sufficient duration to estimate a change in Fulton's condition factors as differences may occur at different times of the year in PIE. Second, measurement of specific landscape features (such as ditches, creek depth, creek width, and water retention) would provide better assessment of landscape changes rather than a somewhat arbitrary division into upper and lower reaches. Landscape feature measurements listed above or other measurements of complexity (similar to Kneib, 2009) may influence growth rate and condition of resident mummichog populations in a fashion similar to Kneib (2009).

A larger question that needs to be addressed is "What is the mechanism of density-dependent reductions in mummichog growth rates in the nutrient-enriched creeks?" Because nutrient enrichment increased abundance of mummichogs, density-dependent effects may be influencing the mummichog population in nutrient-enriched creeks. One cause of the density-dependent effect could be an increase in intraspecific competition. From my data I cannot determine if abundances were greater at the beginning of the field season or if they increased as the nutrient treatment was applied. A better understanding of the population dynamics of mummichogs would help to determine if intraspecific competition is a constant condition throughout the year or a new condition from an increasing abundance with nutrient treatment from a growth response or migration into the creeks. Other

density-dependent mechanisms could also be addressed in determining why growth rate decreases in the nutrient-enriched creeks. Alternative density-dependent mechanisms could be an increased parasite load or altered behavior. Microcosms could help to study mummichog behavior and have been used in past studies (Carson and Merchant 2005) to examine behavior changes in grass shrimp in the presences of predators.

Past studies of mummichogs indicate they generally grow faster during the summer months (Teo and Able 2003). With data I collected, there is no way to know if mummichogs in nutrient-enriched creeks experienced faster growth rates earlier in the season or if growth rate was highest when measured in July and August. Growth rates should also be measured throughout the entire nutrient-enrichment period. The peak growth rates for fertilized creek mummichogs may be reached earlier in the season and then slow due to the increase in mummichog abundance. This would help explain the differences in size classes as well. Without growth rate data from earlier in the season it is impossible to know when mummichog growth rates began to differ or if they were different for the entire season.

A last question to examine, which may have a similar answer to the previous question, is “Are mummichogs changing their diet in the nutrient-enriched creeks?” Nutrient enrichment can provide more food to the mummichog population via bottom-up production increasing the

amount of benthic algae available. Similarly to the behavioral changes mentioned above, mummichogs may change their diet by choosing benthic algae over benthic invertebrates since benthic algae would be more readily available in nutrient-enriched creeks. Lower amounts of protein in the mummichog diet associated with benthic algae could contribute to the slower growth rates in fertilized creeks. Whether this is density dependent or dependent on the abundance of benthic algae remains to be seen. Although the relative rates of herbivory and carnivory are difficult to compare in small fishes, a current diet analysis study is underway which may shed light on this hypothesis (Fleeger, Johnson in preparation).

4.5 – Ecological Impacts

TIDE is a unique study which can be difficult to conduct due to its magnitude and size. TIDE is the only study of its kind where a salt marsh is experimentally nutrient enriched on the entire landscape level. This study suggests the mummichogs benefitted from chronic nutrient enrichment. This may not be a permanent trend, as continuous investigation of these effects in PIE may ultimately show. It is important to measure the effects over multiple years, which TIDE has done in this ecosystem since 2003. Nutrient enrichment has many negative effects on the environment, like sediment loss, hypoxia, vegetation loss, and food-web alterations (NOAA 1999; Deegan 2002). Nutrient enrichment also has known positive and negative effects on

fisheries (NOAA 1999; Jackson et al. 2001; Breitburg et al. 2009), including increasing abundances and biomass. Further study of the mummichog population in following years needs to be conducted to determine if the nutrient enrichment will continue to yield positive results (the observed increasing biomass) or begin trending to possible negative results.

Mummichogs are a high-level predator in PIE salt marshes; therefore, increasing abundances of mummichogs associated with nutrient enrichment can lead to stronger top-down control over lower trophic levels. Populations can increase from bottom-up enrichment, as the mummichogs are doing in TIDE. As the mummichog population increases, the top-down control may increase, perhaps becoming greater than the bottom-up enrichment. Because mummichogs are omnivorous and eat a wide variety of prey, the food web could be drastically altered. Increased predation from mummichogs can decrease the abundances and possibly change size classes of benthic algae, infauna, epifauna, and grass shrimp. This top-down control may prevent lower trophic levels from increasing with nutrient enrichment, aiding in ecosystem resistance to anthropogenic change and increasing ecosystem stability. The research I have done in PIE suggests both top-down and bottom-up forces are of significant importance in this system. My research shows marshes can be susceptible to human influence via nutrient enrichment and altering abundances of top-predators. The long-term

effects and magnitude of these effects should continue to be studied and should be of concern maintaining the stability and resilience of these marine coastal ecosystems.

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